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Three New Species of Aeolid Nudibranchs (Opisthobranchia) from the Pacific Coast of Mexico, Panama, and the Indopacific, with a Redescription and Redesignation of a Fourth Species

SANDRA MILLEN

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada V6T 1Z4
(e-mail: millen@zoology.ubc.ca)

AND

ALICIA HERMOSILLO

Universidad de Guadalajara, Centro Universitario de Ciencias Biológicas y Agropecuarias, Las Agujas, Zapopan, Jalisco, México
(e-mail: alicia_hg@prodigy.net.mx)

Abstract. Three new species of aeolid nudibranchs are described and another species is redescribed and redesignated based on specimens collected at several localities of the tropical eastern and Indopacific. *Dondice galaxiana* sp. nov. is a facelinid aeolid, distinct from other species for its light brown and cream colored body with four dark brown spots containing bright turquoise centers between each cluster of cerata and a few similar spots on the sides. The cerata are light brown or pinkish tan with white cnidosacs and a brown ring below the cnidosacs. They are in raised arch-shaped clusters. The mottled brown and cream oral tentacles are long, the short rhinophores have disk-shaped annulations, and the unarmed penis has a prominent penial gland. The generic placement of another facelinid species was problematic and was therefore assigned as a new genus, *Adfacelina* gen. nov. *Adfacelina medinai* sp. nov. has cerata in arches with multiple rows. The penis is blunt tipped, bearing one outer row of tiny conical spines and there is no accessory gland. The external coloration is pink with opaque yellow blotches covering the body, cerata, rhinophores, and oral tentacles. Our phylogenetic analysis suggests this genus is close to the genera *Dondice* and *Facelina*. *Phestilla hakunamatata* Ortea, Caballer & Espinoza, 2003, is redescribed and placed in the facelinid genus *Hermosita* because it has a cleioproctic anal position, a radula with slender denticles, two bursae, and a fleshy papilla beside the penis. Both the familial and generic placement of the fourth species was problematic. It has the external appearance and notal flange of a flabellinid and the anus is acleioproctic. Internally it has a unidentate radula and the penis is armed with a chitinous spine. External coloration of *Unidentia angelvaldesi* sp. nov. varies with diet from orange shades or white with a series of purple lines and opaque white markings on the body, rhinophores, cerata, and oral tentacles. A phylogenetic analysis suggests that this species should be placed in a new genus, *Unidentia* gen. nov., and that this genus is more closely allied to other uniseriate, acleioproctic aeolids of the genus *Piseinotecus* than members of the family Facelinidae.

Resumen. Se describen tres especies nuevas de nudibranquios aeólidos, una especie más es redescrita y su asignación genérica cambiada con base en especimenes colectados en localidades del Pacífico oriental y el Indopacífico. *Dondice galaxiana* sp. nov. es un aeólido facelinido distinto de otras especies por su coloración café claro y crema con cuatro puntos café oscuro con centros azul turquesa entre cada grupo de ceratas y algunos puntos similares en los laterales. Los ceratas son café claro o rosado con cnidosacos blancos y un anillo café proximal a los cnidosacos. Los ceratas se encuentran en grupos elevados en forma de arco. Los tentáculos orales son largos y moteados de color café y crema; los rinóforos son cortos con anulaciones en forma de discos, la glándula penial es prominente, y el pene no está armado. La asignación genérica de otro facelinido fue problemática por lo que se asignó al género nuevo, *Adfacelina* gen. nov. *Adfacelina medinai* sp. nov. tiene ceratas en arcos de filas múltiples. La punta del pene es chata, con una línea externa de espinas cónicas diminutas sin glándula accesoria. La coloración externa es rosa con manchones amarillo opaco cubriendo completamente ceratas, rinóforos, y tentáculos orales. Nuestro análisis filogenético sugiere que el género es cercano a los géneros *Dondice* y *Facelina*. *Phestilla hakunamatata* Ortea, Caballer y Espinoza, 2003, es redescrita y asignada en el género de facelinido *Hermosita* por tener el ano en posición cleiopróctica, rádula con dentículos delgados, dos bursas, y una papilla carnosa a un lado del

pene. Tanto la asignación genérica como de familia de la cuarta especie fue problemática. Tiene la apariencia externa y falange notal de un flabelinido, el ano siendo acleioprócticо. Internamente tiene rádula uniserrada y el pene armado con una espina quitinosa. La coloración externa de *Unideutia angelvaldesi* sp. nov. varía según su alimentación de tonos anaranjados a blanco con una serie de líneas moradas y patrones de blanco opaco en el cuerpo, rinóforos, cerata, y tentáculos orales. El análisis filogenético sugiere que esta especie debería ser asignada a un género nuevo, *Unideutia* gen. nov. y que este género se encuentra más cercanamente relacionado a los aeólidos acleioprócticos, uniserrados del género *Piseinotecus* que los miembros de la familia Facelinidae.

INTRODUCTION

A survey was undertaken by the junior author of the opisthobranch mollusks of Bahía de Banderas, on the Pacific coast of Mexico. Results indicated 20 range extensions (Hermosillo-González, 2003) and a total of 96 species. Several of these species were undescribed, and additional species have since been added by Hermosillo & Behrens (2005) to a current total of 141 reported by Hermosillo-González (2006). Some ranges were extended further south as a result of a visit to Panama (Hermosillo, 2004; Hermosillo & Camacho-García, 2006).

Subsequent descriptions by Anġulo-Campillo & Valdés (2003), Ortea et al. (2003), Hermosillo & Valdés (2004), Gosliner & Bertsch (2004), Dayrat (2005), Hermosillo & Valdés (2007a, b), and Millen & Hermosillo (2007) have added 13 new species. Photographs of these and several, as yet undescribed, species can be found in three recent books: Behrens & Hermosillo (2005), Camacho-García et al. (2005), and Hermosillo et al. (2006). This paper describes three additional aeolid nudibranch species and redescribes and reassigns the genus of *Phestilla hakumanatata* Ortea, Caballer & Espinosa, 2003 to the genus *Hermosita* Gosliner & Behrens, 1986.

The four species in this paper have a uniseriate radula and a jaw with one row of denticles on the masticatory margin. Three of the species have the anus in the cleioproctic position (among the posterior cerata) and belong in the family Facelinidae Bergh, 1890. The other species has its anus in the interhepatic area, in an acleioproctic position, an anterior notal brim, and well-developed ramified oral glands, all features that are not found in the Facelinidae. It has been placed in the family Unidentidae fam. nov. and assigned a new genus, *Unidentia* gen. nov.

MATERIALS AND METHODS

Collection and observations were conducted by scuba diving and intertidally. The material examined is deposited at the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), the Malacology Section of the Natural History Museum of Los Angeles County (LACM), and the Museum of Zoology of the University of Costa Rica (MZUCR-INB).

Specimens were relaxed in a 7% magnesium chloride solution in freezing seawater and preserved in 70% ethanol. Specimens were dissected by a right lateral incision from back to front just above the foot, and the internal features were examined and drawn using a dissecting microscope with a camera lucida. The buccal mass was removed and placed in 10% sodium hydroxide until the radula and jaws were isolated from the surrounding tissue. The radula and jaws were then rinsed in water, dried, and mounted for examination. Scanning electron micrographs were made with a Hitachi S-4700FE scanning electron microscope.

Features of living animals were recorded in the field by digital photography, both *in situ* and in aquarium photographs with a Nikon Coolpix 995 camera. For underwater photography, a YS-90 Sea and Sea and an INON slave strobe were used, with white balance set on daylight. For aquarium photographs, only the INON slave strobe was used with the same white balance setting. No color correction was used.

SPECIES DESCRIPTIONS

Family FACELINIDAE Bergh, 1890

Genus *Dondice* Marcus, Er. 1958

Dondice galaxiana Millen & Hermosillo, sp. nov.

(Figures 1A, F, 2, 3)

Material: Holotype: CASIZ 176810, 7 mm long, Puerto Vallarta, Noche Iguana, Bahía de Banderas, 28 April 2002, at 15 m depth on a rock wall. Collected by S. Millen. **Paratypes:** LACM 3042, 5 mm long, Mismaloya, Bahía de Banderas, 8 March 2004, at 17 m depth. LACM 194198, 5 mm long, Île Clipperton, 19 April 2007, at 70–90 m depth on a coral detritus slope. Collected by Jeff Bozanic. MZUCR-INB0001496600, 1 specimen, 4 mm long, Roca la Viuda, Puntarenas, Costa Rica, 26 January 1998, at 7–10 m depth. Collected by A. Berrocal. **Other material:** 2 specimens, 6 and 5 mm, dissected, collected with the holotype. 1 specimen, 4 mm, Mismaloya, Bahía de Banderas, 13 June 2004. 1 specimen, 7.5 mm, Mismaloya, Bahía de Banderas, 26 May 2004.

Etymology: The specific name of this species, *galaxiana*, is given because of its otherworldly appearance.

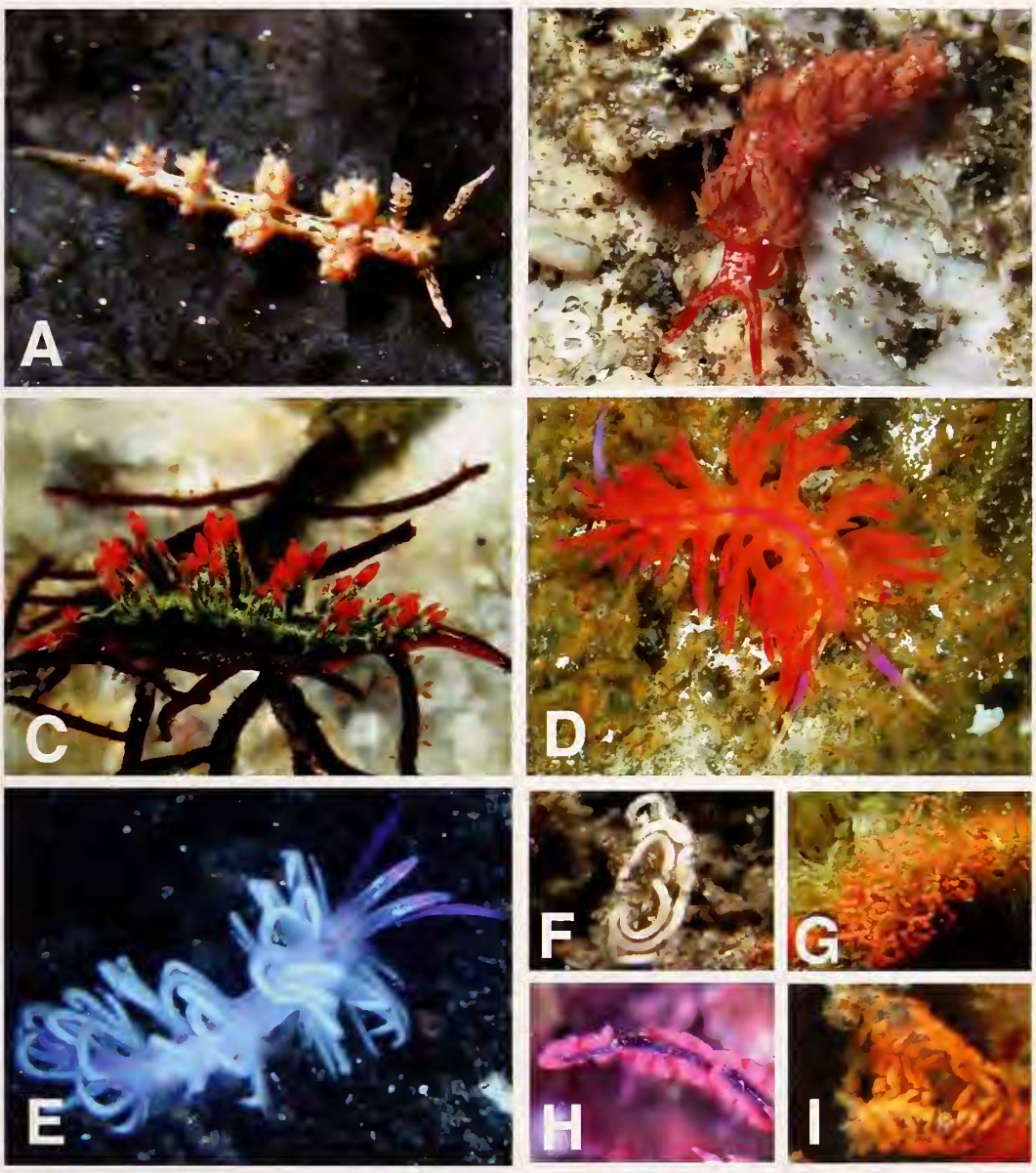

Figure 1. Photographs of living aeolids taken in the field: **A**, *Dondice galaxiana* sp. nov., 8 mm long, Bahía de Banderas, Mexico; **B**, *Adfacelina medinai*, 11 mm long, specimen (CASIZ 175779) from Bahía de Banderas, Mexico; **C**, *Hermosita hakunamatata* from Bahía de Banderas, Mexico; **D**, *Unidentia angelvaldesi*, dark variation (CASIZ 176809), specimen from Bahía de Banderas, Mexico; **E**, *Unidentia angelvaldesi*, pale variation, specimen from Tulamben, Bali; **F**, Spawn of *D. galaxiana*; **G**, Spawn of *A. medinai*; **H**, Spawn of *H. hakunamatata*; **I**, Spawn of *U. angelvaldesi*, dark variation.

External morphology: This aeolid reaches up to 7.5 mm in preserved length. Living size: 8 mm, 1 mm wide, and 1.25 mm high (Figures 1A, 2A). The body is slender, with laterally bulging areas at the clusters of cerata. The rhinophores are short, ending with a cylindrical tip. There are usually 6 or 7 (4–8) large dish-shaped annulations, continuous anteriorly, widest laterally and notched posteriorly. The oral tentacles are slightly longer than the rhinophores, cylindrical and slender. They originate dorsal to the oral surface. The cerata are arranged in tight horseshoe-shaped clusters on raised cushions. The anterior-most two have up to 20 cerata in alternating double rows, whereas the other arches have one row of cerata. There is one precardiac cluster and two to three posterior ones plus a row of 2–3 cerata. The cerata are slender and cylindrical, up to 3 mm in length, with long pointed cnidosacs and granular cores (Figure 2B). The head is oval, slightly

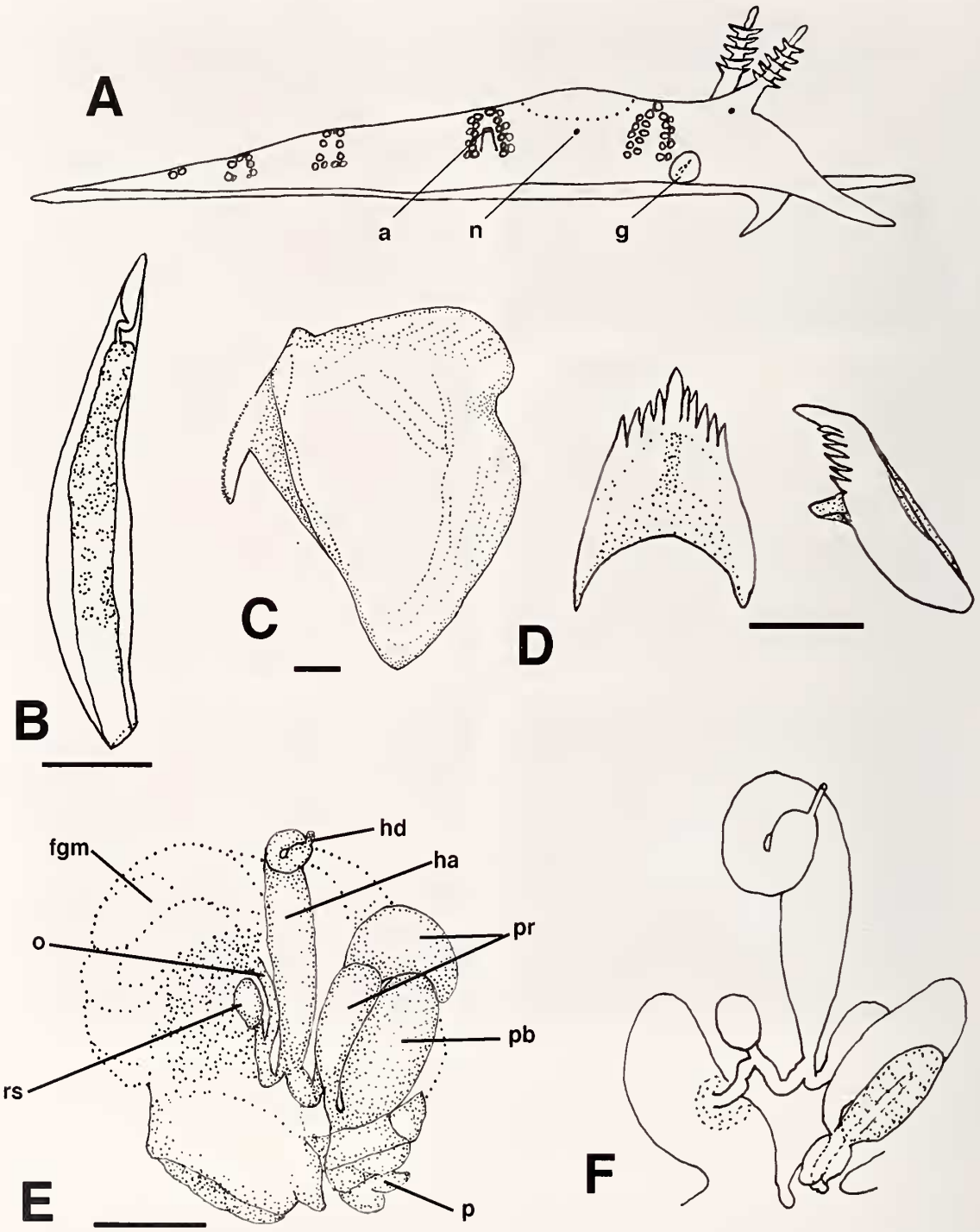

Figure 2. *Dondice galaxiana* sp. nov. from Bahía de Banderas, Mexico: **A**, Right lateral view showing position of ceratal insertions, stylized drawing; **B**, Ceras; **C**, Onc jaw; **D**, Radular tooth; **E**, Camera lucida drawing of the reproductive system; **F**, Stylized drawing of the reproductive system. Abbreviations: **a**, anus; **fmg**, female gland mass; **g**, genital apertures; **ha**, hermaphroditic ampulla; **hd**, hermaphroditic duct; **n**, nephroproct opening; **o**, oviduct; **p**, penis; **pb**, penial bulb; **pr**, prostate; **rs**, receptaculum seminis. Scale bars: B = 0.5 mm; C = 0.1 mm; D = 50 μm; E = 0.5 mm.

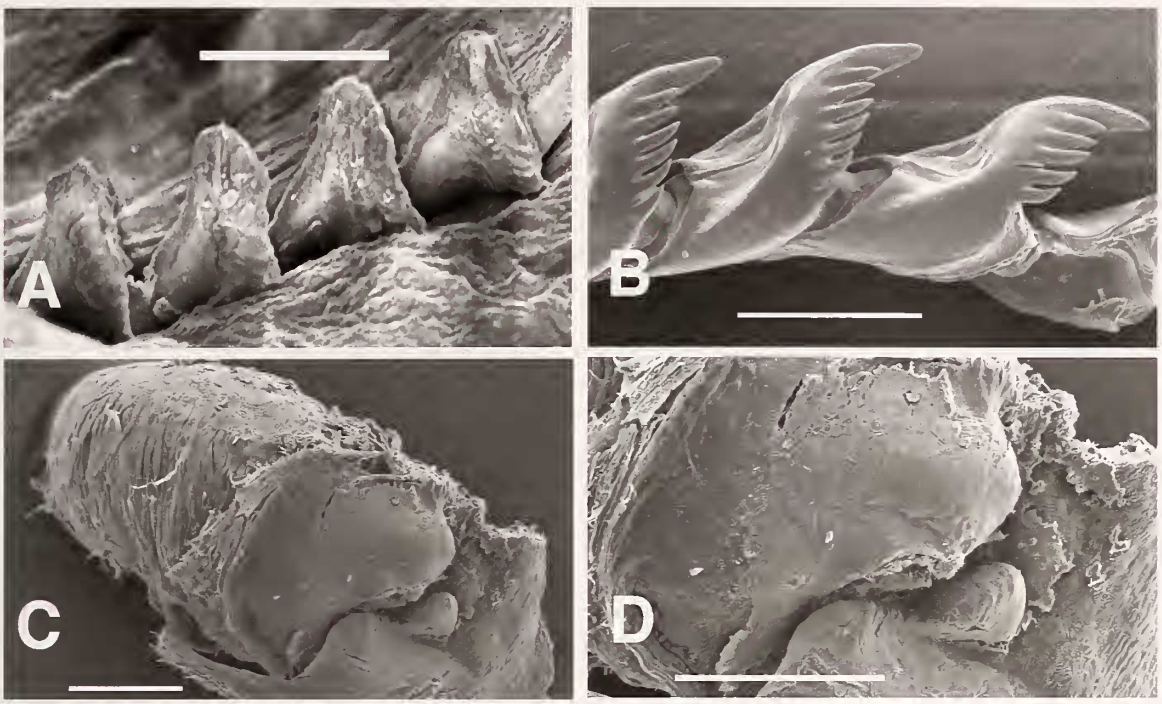

Figure 3. Scanning electron micrographs of *Dondice galaxiana* sp. nov. from Bahía de Banderas, Mexico: **A**, Denticles on masticatory flange of a jaw; **B**, Radular teeth; **C**, Penis and penial sac; **D**, Close-up of penis. Scale bars: A = 10 µm; B = 50 µm; C = 100 µm; D = 100 µm.

wider than long; the mouth is a vertical slit. The foot is bilabiate but not notched and extended into well-defined propodial tentacles up to 1 mm in length. The foot is narrow; each flange is as wide as the attached portion. The portion of the foot posterior to the body cavity is pointed, 1.5 mm long, flat and slender. A diagonal flap separates the genital openings and there is a posteriorly directed, triangular flap anterior to them. They are located below and anterior to the anterior most limb of the prehepatic ceratal arch. The anus is cleioproct, located within the first posthepatic arch. The renal opening is just under the heart, midway in the interhepatic space.

Coloration: The body color is translucent cream with rhomboid-shaped patches on the dorsum between the cerata. The center of each rhombus is light opaque cream surrounded by a light brown band and contains four equidistant bright turquoise spots forming a square. Next to each of these turquoise spots, there is a larger dark olive to black spot. In some specimens, the turquoise spots are so faint they can barely be distinguished next to the dark spots. The rest of the body is covered with random bright white specks, the number varying among specimens, with some completely devoid of them. The sides of the body have dark reddish brown patches that join near the cerata, further defining the rhombus. Some light cream patches with dark brown spots are also found on the sides. The cerata are light pinkish brown with a subterminal brown band and darker reddish brown cores. The surfaces of the cerata are covered with random white spots. The rhinophores have a clear base followed by a brown area and an opaque cream club. The head, at the base of the rhinophores, is clear, allowing the dark eyes to be seen. The remaining cephalic area follows the same coloration pattern as the body. The oral tentacles are the same color as the body, with dark brown irregular blotching at the bases and lighter blotching along the length, ending with clear tips.

Internal anatomy: The buccal mass has a muscular lip disk with a thin, chitinized ring. There are no compound oral glands, but solitary labial glands surround the mouth. The jaws (Figure 2C) are covered with black melanophores in the epithelium, concentrated dorsally and ventrally. They are pale yellow with a notched posterior margin.The masticatory margin bears a single row of approximately 20 well-developed, triangular denticles (Figure 3A).

The radular formula is 15–16 (1); the teeth are amber colored and located in a slightly protruding radular sac. Each rachidian tooth has an elongate cusp bearing one or two denticles and there are 4–6 triangular denticles

flanking the cusp (Figures 2D, 3B). The teeth are approximately 110 μm in length. The salivary glands have a long, narrow duct and are large with a flattened, irregular shape. The esophagus is a short tube leading into a large, oval, striated stomach. The posterior hepatic duct lies dorsal to the ovotestis, the wide, striated intestine forms a deep U along the side of the ovotestis and ends at the anus, located high within the first posterior hepatic arch.

The central nervous system has large, oval, fused cerebropleural ganglia, connected closely together by a narrow commissure. There are short stalks to large rhinophoral ganglia in the bases of the rhinophores. The eyes are almost sessile. Small statocysts lie behind each eye. The oval pedal ganglia are about half the size of the cerebropleurals and connected to them by a short commissure and to each other by a longer commissure. The smaller, oval buccal ganglia lie beneath the esophagus and are connected to each other by a moderately long commissure.

The ovotestis is composed of smooth grape-like lobules containing both male and female acini. The long, narrow ovotestis duct widens slightly into a tubular ampulla, which runs the length of the female gland mass and then bifurcates into an oviduct and a vas deferens (Figure 2E, F). The vas deferens immediately becomes prostatic, with a wide glandular portion looping against and entering the base of a large penial sac. The penial sac and prostate appear as one structure. The penial sac is smooth and muscular externally; internally it is glandular with a central hollow. The sac and vas deferens terminate in a short, blunt, muscular, unarmed penis. When everted, the vas deferens projects anteriorly with a posterior bulge and a lateral flap. The oviduct enters a small, round, seminal receptacle and then continues a short distance to enter the female gland mass. The female gland mass is convoluted and white with a central, folded, bright yellow albumen gland.

Natural history: This species is known from Bahía de Banderas, Île Clipperton (Kaiser, 2007) and Costa Rica (Camacho-García et al., 2005). It is found in the shallow subtidal, under or over rocks with good hydroid coverage, from March to June in Bahía de Banderas. It has been photographed eating a reddish-orange athecate hydroid, possibly *Endendrium*. The egg mass, observed in May, is a white string coiled around the hydroid (Figure 1F).

Discussion: The genera of Facelinidae having multiple rows of arch-shaped cerata on pedicles and no penial armature are listed in Millen & Hamann (1992: table 1). None of these genera exactly fit the present species, nor do any of the genera with arches bearing a single row of cerata. The rhinophores of this species are unusual in their cup-like annulations, similar to those of *Nanuca* Marcus, 1957. *Dondice galaxiana* differs from *Nanuca* in the ceratal arrangement, the presence of propodial tentacles, heart and kidney, and in arrangement of the reproductive system. The jaws have external black pigment, one row of masticatory denticles, and a posterior notch, as is found in *Caloria elegans* (Alder and Hancock, 1845) and *Dondice occidentalis* (Engel, 1925). *Caloria* Trinchese, 1888, has cerata in rows and simple rhinophores, whereas *Dondice* has weakly annulate rhinophores and multiple rowed arches on pads. The genus *Dondice* is unique in that it has a penial gland and a large penis containing the prostate. This new species has a prostate stuck against the penial bulb and entering the distal part of the penial bulb. In *D. occidentalis* and the similar *Dondice parguarensis* Brandon & Cutress, 1985, there is an external sperm groove spiraling down the penis to the tip, covered by a flap (personal observation, Millen), whereas in the new species, the penial bulb and prostate join distally and the short, muscular penis extends from the penial bulb. This species is provisionally placed in the genus *Dondice,* which is the only genus with cerata in arches with multiple rows and having a separate, unstalked penial gland and unarmed penis. They also are similar in that the jaws are notched and covered with black tissue and the teeth have pointed, denticulate cusps and lateral denticles. Penial glands are also found in the genus *Facelina* Alder and Hancock, 1855, which has cerata in rows and simple arches, but the penial glands in this genus enter the penial sac and are quite different in shape being bulbous with a long stalk.

Family Facelinidae Bergh, 1890

Genus *Adfacelina* Millen & Hermosillo, gen. nov.

Generic diagnosis: Cleioproctic aeolids with lamellate rhinophores and well-developed propodial tentacles. Pre- and postcardiac cerata in arches with multiple rows of cerata. Uniseriate radula with a prominent cusp and several strong lateral denticles. Jaw with one row of denticles on the masticatory margin and without a posterior notch. One copulatory bursa. Penis wide, with a blunt, lobate tip, bearing one outer row of tiny papillae.

Etymology: The name *Adfacelina* underscores the fact that this species has a series of papillae in a position similar to the chitinous spines of *Facelina*.

Type species: *Adfacelina medinai* Millen & Hermosillo sp. nov.

Adfacelina medinai Millen & Hermosillo, sp. nov.

(Figures 1B, G, 4, 5)

Material: Holotype: CASIZ 176806, 14 mm, Islas Marietas, Bahía de Banderas, 20 December 2003, collected by A. Hermosillo. **Paratypes:** LACM 3043,

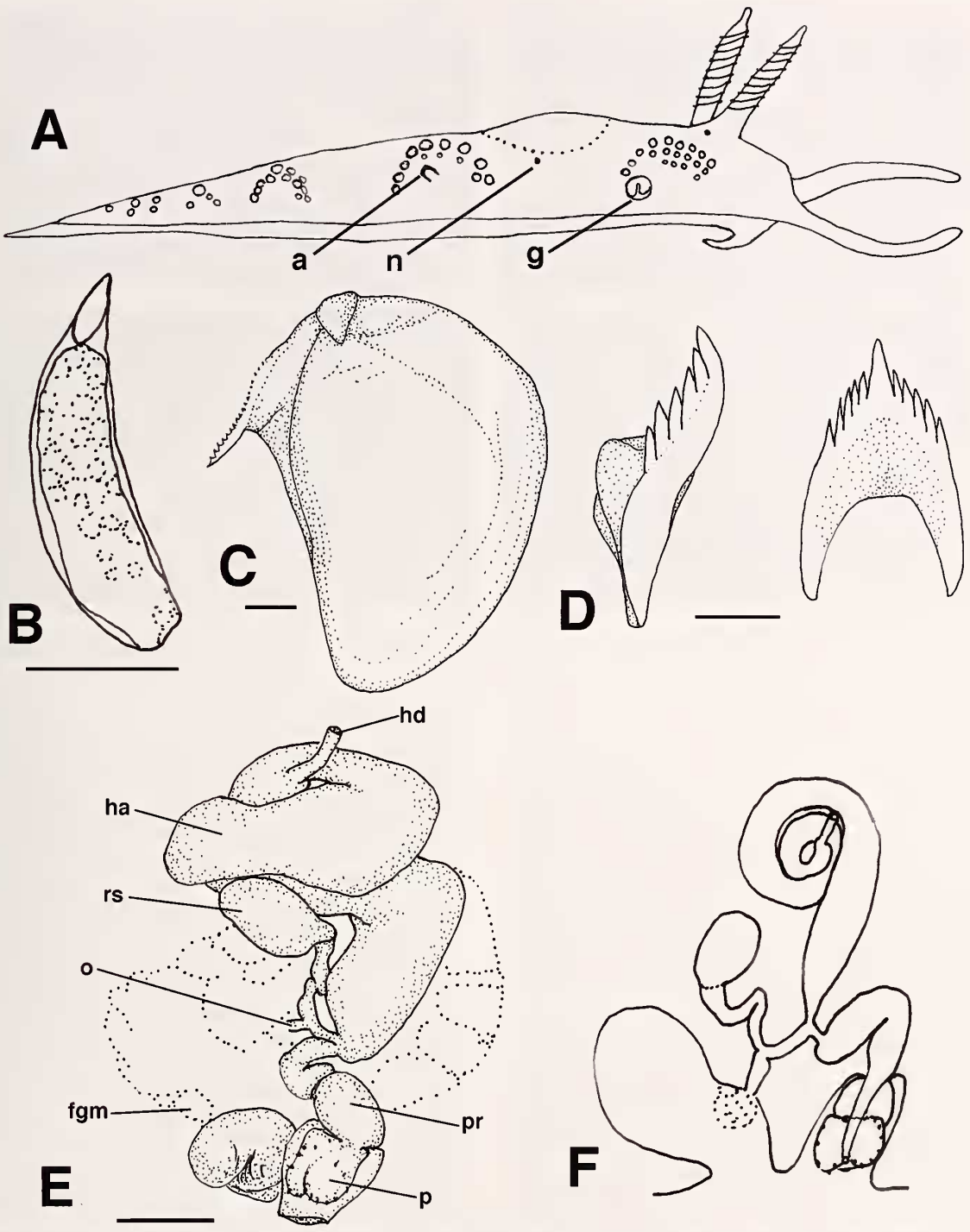

Figure 4. *Adfacelina medinai* sp. nov. from Bahía de Banderas, Mexico: **A**, Right lateral view showing position of ceratal insertions, stylized drawing; **B**, Ceras; **C**, One jaw; **D**, Radular tooth; **E**, Camera lucida drawing of the reproductive system; **F**, Stylized drawing of the reproductive system. Abbreviations: **a**, anus; **fgm**, female gland mass; **g**, genital apertures; **ha**, hermaphroditic ampulla; **hd**, hermaphroditic duct; **n**, nephroproctic opening; **o**, oviduct; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis. Scale bars: B = 0.5 mm; C = 0.1 mm; D = 50 μm; E = 0.5 mm.

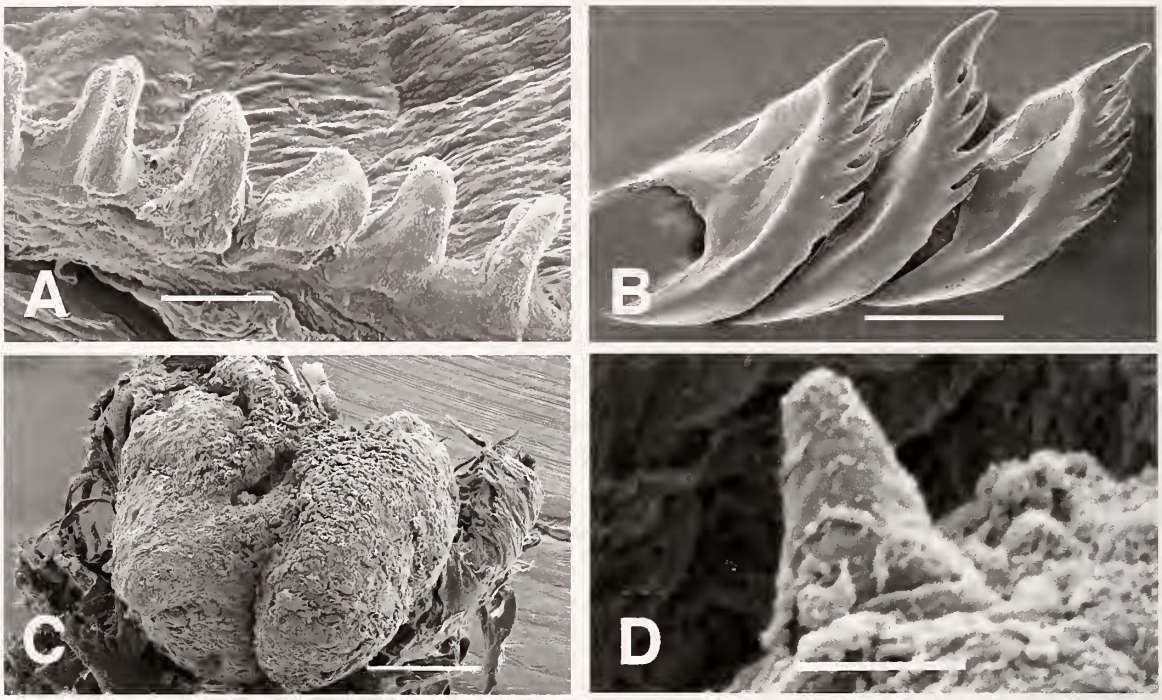

Figure 5. Scanning electron micrographs of *Adfacelina medinai* sp. nov. from Bahía de Banderas, Mexico: **A**, Denticles on masticatory flange of a jaw; **B**, Radular teeth; C, Penis showing its double structure and single row of papillae; **D**, Close-up of one penial papilla. Scale bars: A = 15 μm; B = 50 μm; C = 50 μm; D = 10 μm.

8 mm long, Islas Marietas, Bahía de Banderas, 29 May 2004 at 12 m depth, collected by A. Hermosillo. LACM 174197, 1 specimen, 5 mm, Île Clipperton, 18 April 2007, 93 m depth, collected by J. Bozanic. CASIZ 175779, 2 specimens, 11 mm long, 1 dissected, Islas Marietas, Bahía de Banderas, 12 April 2004. **Other material:** 1 specimen, 5 mm, 11 January 2003, Noche Iguana, Bahía de Banderas, dissected, collected by Alicia Hermosillo. 1 specimen, 9.5 mm, 10 June 2003, Islas Marietas, Bahía de Banderas, dissected, collected by Alicia Hermosillo.

Etymology: *Adfacelina medinai* is named in recognition of our friend Pedro Medina Rosas, who has been a dive and work partner of Alicia Hermosillo from day one. This species has been found in great depths (Île Clipperton) and inside sea caves (Bahía de Banderas), facts that are also a reminder of Pedro's experience as a technical diver.

External morphology: This aeolid reaches up to 14 mm in preserved length, 18 mm live length (Figure 1B). A 9.5-mm preserved specimen was 1.8 mm in width and 2 mm high. The rhinophores are 2 mm long, with a long, slender tip and up to 9–11 irregular perfoliations. The perfoliations have a small gap anteriorly and meet posteriorly. They are much wider on the sides and resemble annulations. The cerata are arranged in shallow arches on raised cushions (Figure 4A). The anterior-most, precardiac arch has a triple row anteriorly and a single or double row posteriorly. The first postcardiac arch has a double row anteriorly in the arch and a single or double row posteriorly. Subsequent arches usually have single rows of cerata. There are up to six postcardiac arches followed by a small posterior raised row and often a few cerata. The cerata are thick cylinders, up to 2 mm in length, with tiny pointed tips. The hepatic cores are wide and the cnidosacs are long and slender (Figure 4B). The broad head is a wide oval shape, the mouth a vertical slit. The head indents slightly anteriorly. The stout oral tentacles are 2.5 mm long, slightly longer than the rhinophores. They are flattened ventrally and are wider at the base. They originate at the oral surface and are held anterior-laterally. The foot is bilabiate and indented below the mouth. It is extended into stout, 1.2-mm-long, propodial tentacles. The foot is narrow at the middle attached portion with moderately wide lateral flanges, with a long, cylindrical, slender, 1-mm-long, trailing portion. The anus is cleioproct, located midway within the first posthepatic arch. The renal opening is slightly posterior to the middle of the interhepatic space.

Coloration: The coloration of the body is orange or reddish pink with irregular opaque yellow blotches

and spots covering it uniformly. The rhinophores are yellow with a medial dark pink band. There is a pinkish-orange area at the base of the rhinophores where the dark eyespots can be observed. The oral tentacles are long, with a dark pink medial band spotted with yellow and lighter towards the tip. The cerata are orange-red, covered with irregular opaque yellow blotches with a distal deep reddish-pink ring, just below the clear cnidosacs. The cephalic area is darker pink than the rest of the body, with the same yellow blotches.

Internal anatomy: The buccal mass has a short muscular oral tube with tiny labial glands attached. No compound oral glands were seen. There is a thin, round, chitinized lip disk in front of the jaws. The jaws (Figure 4C) are oval and pale yellow. They have a long masticatory margin with a single row of 18–22 well-developed denticles, which increase in size distally (Figure 5A).

The radular formula is 19–25 (1). The teeth are pale yellow and originate in a barely projecting radular sac. Each tooth has an elongate cusp, and 4–5 triangular denticles flanking the cusp (Figures 4D, 5B). The teeth are approximately 150 μm in length. The salivary glands are large irregular clusters located between the stomach and genital system. They have slender ducts that adhere to either side of the esophagus and insert on the buccal bulb. The esophagus is a wide, long cylindrical tube leading into a large, flattened, oval stomach. The posterior hepatic duct lies dorsal to the ovotestis. The intestine forms a long, shallow arch along the side of the ovotestis and ends at the anus, located high within the first posterior hepatic arch.

The central nervous system has large, oval, fused cerebropleural ganglia connected closely together by a narrow commissure. There are short nerves leading to round rhinophoral ganglia in the base of the rhinophores. The black eyes are almost sessile. Small statocysts lie directly behind each eye. The oval pedal ganglia are as long as the cerebropleural ganglia but only half as wide. They are connected by a short commissure to the cerebropleural ganglia and by a wide, longer commissure to each other beneath the esophagus. The smaller, round buccal ganglia lie beneath the esophagus and are connected to each other by a short commissure.

The ovotestis is composed of clusters with several tiny female acini peripheral to larger sac-like male acini, each with a small ductule leading to the hermaphroditic duct. The reproductive system is illustrated in Figure 4E, F. The hermaphroditic ampulla is swollen and folds back on itself and around, then down the length of the female gland mass. The ampulla then splits into the vas deferens and oviduct without a distinct postampullar duct. The oviduct is narrow and extends dorsally posterior to the base of the ampulla. It is joined by a duct from the semiserially arranged, oval, receptaculum seminis and then continues a short distance to enter the albumen (capsule) gland. There is no bursa copulatrix, nor a separate vagina. The female gland mass has a small albumen gland and complex, coiled membrane and mucous glands. The vas deferens immediately swells into a wide, short prostate, which enters the male atrium. The penis is wide and rounded at the tip. Two blunt lobes surround the vas deferens opening in the center, and each lobe bears one row of tiny papillae along the rim, although in one specimen the penis was even more inflated and the tip appeared as one slightly indented disk (Figure 5C, D). The penis appears to be glandular inside. The papillae are firm but fleshy with rounded bases embedded in the head of the penis, which stain differently than the penis itself. No accessory glands were seen. A small ridge separates the two genital openings. They are located below the posterior most limb of the first arch.

Natural history: This species is known only in Bahía de Banderas, Pacific coast of Mexico and Île Clipperton (Kaiser, 2007), where only one specimen was collected. The rest of the specimens have been found under rocks or inside a sea cave during the months of January, April, May, June, and December. The egg mass (Figure 1G) is pink, laid in irregularly folded strings upon an unidentified hydroid in the months of March and April.

Discussion: This animal belongs in the family Facelinidae with those species that have cerata arranged in arches both anteriorly and posteriorly and the arches are raised and consist of multiple (1–3) rows of cerata. Three genera in this family have tiny chitinous spines: Facelina, *Amanda* MacNae, 1954, and *Echinopsole* MacNae, 1954. *Amanda* is represented only by its type species, *A. armata* MacNae, 1954, and differs from this new species by its rounded foot corners, simple arches, and sparse, annulate cerata. The reproductive system has more prominent, chitinous hooks encircling the opening. The penis of *Facelina* is similar, but has a bulbous penial gland. *Echinopsole* is represented by two species, the type species, *E. fulvus* MacNae, 1954, and *E. breviceratae* Burn, 1962. This genus has multiple cerata in arches, but has many rows of chitinous spines on the penis, a small accessory gland, and annulate rhinophores. None of these genera appears to fit the new species, which has fleshy papillae. Fleshy papillae are found in *Caloria elegans*, which has its cerata in rows. This species differs from all of the current members of the family by its possession of cerata in multiple arches, penial armature, and its lack of an accessory penial gland; we have placed the new species in its own genus, *Adfacelina*.

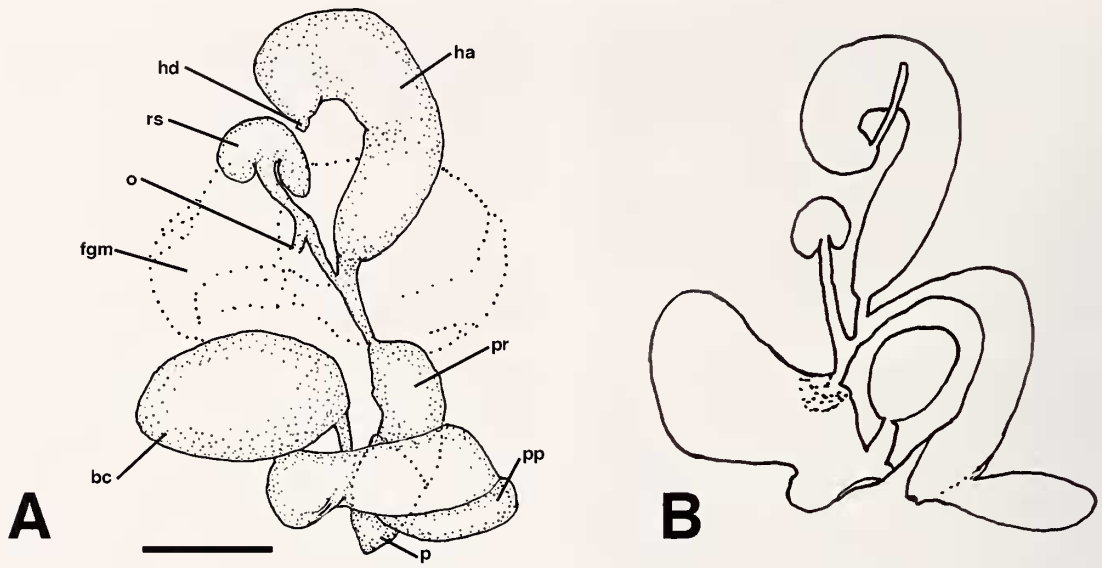

Figure 6. *Hermosita hakunamatata* (Ortea, Caballer, & Espinosa, 2003) comb. nov. from Bahía de Banderas, Mexico: **A**, Camera lucida drawing of the reproductive system; **B**, Stylized drawing of the reproductive system. Abbreviations: **bc**, bursa copulatrix; **fgm**, female gland mass; **ha**, hermaphroditic ampulla; **hd**, hermaphroditic duct; **o**, oviduct; **p**, penis; **pp**, penial papillae; **pr**, prostate; **rs**, receptaculum seminis. Scale bar: A = 0.5 mm.

Family Facelinidae Bergh, 1890

Genus *Hermosita* Gosliner & Behrens, 1986

Hermosita hakunamatata (Ortea, Caballer & Espinosa, 2003), comb. nov.

(Figures 1C, H, 6)

Phestilla hakunamatata Ortea, Caballer & Espinosa, 2003: 137–141, plate 1C, figures 3, 4C.

Material: Voucher specimens: LACM 173657, 1 specimen, 9 mm, Cerro Pelon, Isla Isabela, Bahía de Banderas, 14 December 2002, collected by Alicia Hermosillo. CASIZ 176805, 1 specimen, 9 mm, Cerro Pelón, Isla Isabela, Bahía de Banderas, 14 December 2002, with spawn, collected by Alicia Hermosillo. **Other material:** 7 specimens, Islas Marietas, Bahía de Banderas, 13 June 2003, collected by Alicia Hermosillo.

External morphology: This animal has been well photographed: Ajtai, in Rudman (2002) as *Flabellina* sp. 3; Hermosillo-González (2003) as *Flabellina* sp.; Ortea et al. (2003: plate 1C); Behrens & Hermosillo (2005: species #279, p. 122). The external description was based entirely on the type specimen, which is figured by Ortea et al. (2003) as figure 4C.

Internal anatomy: The radula and jaws of the type specimen were described and illustrated by Ortea et al. (2003: figures 3A, B, C). The remainder of the digestive tract, central nervous system, and reproductive systems were not examined and are described here for the first time.

The buccal opening is thick and muscular. Ventrally, ramified oral glands extend under the rounded buccal mass. The jaws are light yellow with smooth masticatory edges as illustrated by Ortea et al. (2003).

The radula formula is 12–15 (1) and the teeth are as illustrated by Ortea et al. (2003) with 5–14 long denticles per side. The salivary glands are small and round with a short, slender duct. They are located lateral to the buccal ganglia and are only slightly larger than each ganglion. The esophagus is a long, thin tube. The stomach is large and round or oval, the anterior hepatic ducts branching off the anterior portion. The intestine leaves the right side as a long, broad tube, looping down slightly before extending dorsally and narrowing just before the anus. The anus is in the cleioproct position on a small papilla within the first postcardiac arch and opposite the third ceras. The posterior hepatic duct runs ventrally with alternating branches beginning on the left. The hepatic branches run up the sides and between the clusters of acini to form horseshoe-shaped arches.

The central nervous system consists of fused, oval, cerebropleural ganglia connected by a short, wide commissure. The rhinophoral ganglia are large, lying at the bases of the rhinophores and are almost sessile. Large black eyes are on short optic nerves. Statocysts are directly behind the eyes at the junction of the pedal ganglia. The oval pedal ganglia are almost as large as the cerebropleurals and are connected to them by a short stalk. They are connected to each other by two longer, narrow cerebro-esophageal commissures. The small, round buccal ganglia lie close to each other beneath the esophagus.

The ovotestis forms a series of semicircular, somewhat flattened, clumps of acini. Each clump is joined by a short, narrow duct to the main collecting duct, which runs on top of the posterior hepatic duct, and to its right, anterior to the acini. This preampullar duct swells to form the hermaphroditic ampulla at the female gland mass (Figure 6). The long, sausage-shaped ampulla is curved. It splits into an oviduct and a vas deferens. The short oviduct is joined by the long duct of the receptaculum seminis, before inserting into the female gland mass. The receptaculum is usually only slightly swollen, but in one specimen was swollen into a small kidney-shaped sac. There is a separate, large, round bursa copulatrix with a short duct opening into the female gonopore. The oviduct enters the large, granular albumen gland. Eggs pass from the albumen gland to the highly convoluted membrane gland and thence to the larger, less convoluted mucous gland, which has anterior and posterior folds. The mucous gland exits at the female gonopore ventral to the duct of the bursa copulatrix. The vas deferens expands into a short, prostatic portion, which enters the penial sheath and slowly tapers to form a blunt, conical penis. There is no clear division between the prostatic portion of the vas deferens and the glandular penis. On the anterior side of the male gonopore is a disk-shaped, rounded, fleshy papilla, which can vary in its extension.

Natural history: *Hermosita hakumamatata* is found living and feeding on the hydroid *Solanderia* sp., which is dark purple with pink polyps. This hydroid lives in the undersides of overhangs on walls. In Bahía de Banderas, it has been found year-round in only a few sites. *Hermosita hakumamatata* is very cryptic in its habitat, particularly smaller specimens with darker coloration. The egg mass (Figure 1H) appears as rose-colored strings, which are laid in December on the distal part of the hydroid (see also Behrens & Hermosillo, 2005: species #279, p. 122).

Discussion: Ortea et al. (2003), having only one incompletely dissected specimen, believed the anus to be in an acleioproct position, posterior in the interhepatic space. Indeed, there is a prominent opening in this position, which upon dissection was revealed to be the nephroproct. The rather inconspicuous anal opening is in the cleioproct position, high within the first postcardiac arch. This error in anal position led Ortea et al. to place this species in the acleioproct family Tergipedidae Bergh, 1889, genus *Phestilla* Bergh, 1874. It is clear that this animal belongs in the family Facelinidae, as it has a cleioproct anus and uniseriate radula with cuspidate teeth. The ceratal groups are in simple arches and the presence of both a proximal, semiserial receptaculum seminis and a distal bursa copulatrix place it in the genus *Hermosita* Gosliner & Behrens, 1986. Other characteristics shared with *Hermosita* are the short prostate, which continues into the penis, an anterior penial flap, long denticles on the radular teeth, and perfoliate rhinophores. *Hermosita sangria* Gosliner & Behrens, 1986, is the only known species in the genus. It also occurs on the hydroid *Solanderia* sp. and is found just slightly north of this species' known distribution, on the outer coast of Baja California. Both species have reddish bodies, but can be distinguished as *Hermosita sangria* is larger (to 70 mm vs. 22 mm), has a violet cast to the body and lower half of the cerata, and a red band followed by yellow or white on the upper half of the cerata, foot corners, oral tentacles, and rhinophores. Internally it has a smooth masticatory margin to the jaw. *Hermosita hakumamatata* has no violet cast to the reddish body and has dark brown and golden spots on the foot, sides, dorsum, and lower half of the cerata. Brown spots are absent in two longitudinal strips between the cerata and are more prominent in smaller animals. The upper halves of the cerata are red, tipped with white cnidosacs. The rhinophores and oral tentacles, except for the most basal portion, lack brown and gold specks and are red with pale yellowish-white tips. The masticatory margin of the jaw bears one row of denticles.

Family UNIDENTIDAE Millen & Hermosillo, fam. nov.

Genus *Unidentia* Millen & Hermosillo, gen. nov.

Family diagnosis: Acleioproctic aeolids with smooth rhinophores, a raised anterior notal flange, and long propodial tentacles. Cerata in rows. Radula uniseriate. Oral glands present. Reproductive system with one proximal and no distal bursa. Penis armed with a long, curved, hollow chitinous stylet.

Generic diagnosis: With the characteristics of the family.

Etymology: The name of genus *Unidentia* Millen & Hermosillo gen. nov. is derived from the Latin *uni*, which means 'one', and *dentis*, which means 'tooth', calling attention to the fact that this flabellinid has a uniseriate radula combined with an acleioproctic anal position.

Type species: *Unidentia angelvaldesi* Millen & Hermosillo sp. nov.

Unidentia angelvaldesi Millen & Hermosillo, sp. nov.

(Figures 1D, E, I, 7, 8)

Material: Holotype: CASIZ 176809, 9 mm long, Los Arcos, El Bajo del Cristo, Bahía de Banderas, 12 June 2003, at 18 m depth, collected by A. Hermosillo.

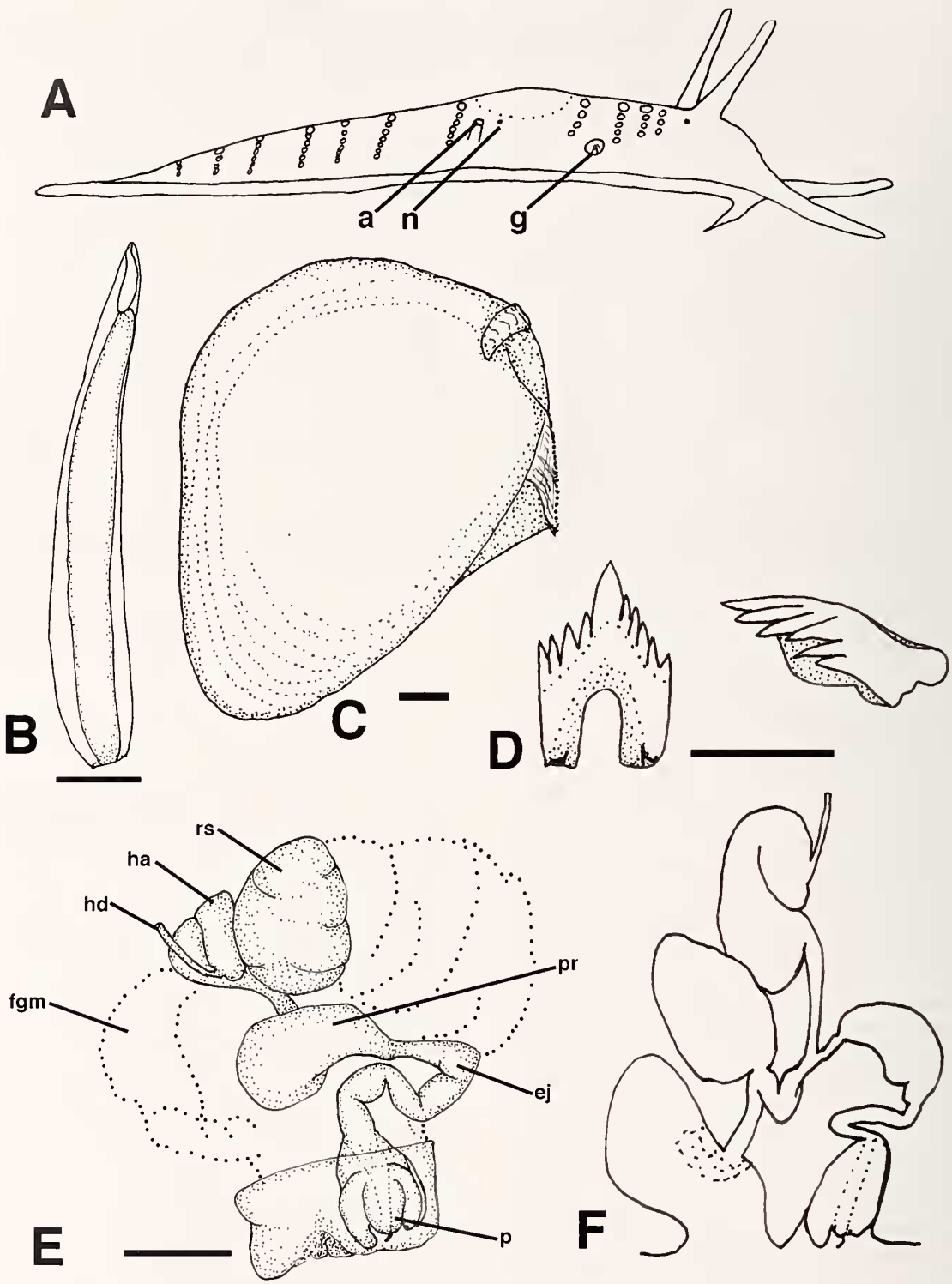

Figure 7. *Unidentia angelvaldesi* sp. nov. from Bahía de Banderas, Mexico: **A**, Right lateral view, showing position of ceratal insertions, stylized drawing; **B**, Ceras; **C**, One jaw; **D**, Radular tooth; **E**, Camera lucida drawing of the reproductive system; **F**, Stylized drawing of the reproductive system. Abbreviations: **a**, anus; **ej**, ejaculatory duct; **fgm**, female gland mass; **g**, genital apertures; **ha**, hermaphroditic ampulla; **hd**, hermaphroditic duct; **n**, nephroproctic opening; **p**, penis; **pr**, prostate; **rs**, receptaculum seminis. Scale bars: B = 0.5 mm; C = 0.1 mm; D = 50 μm; E = 0.5 mm.

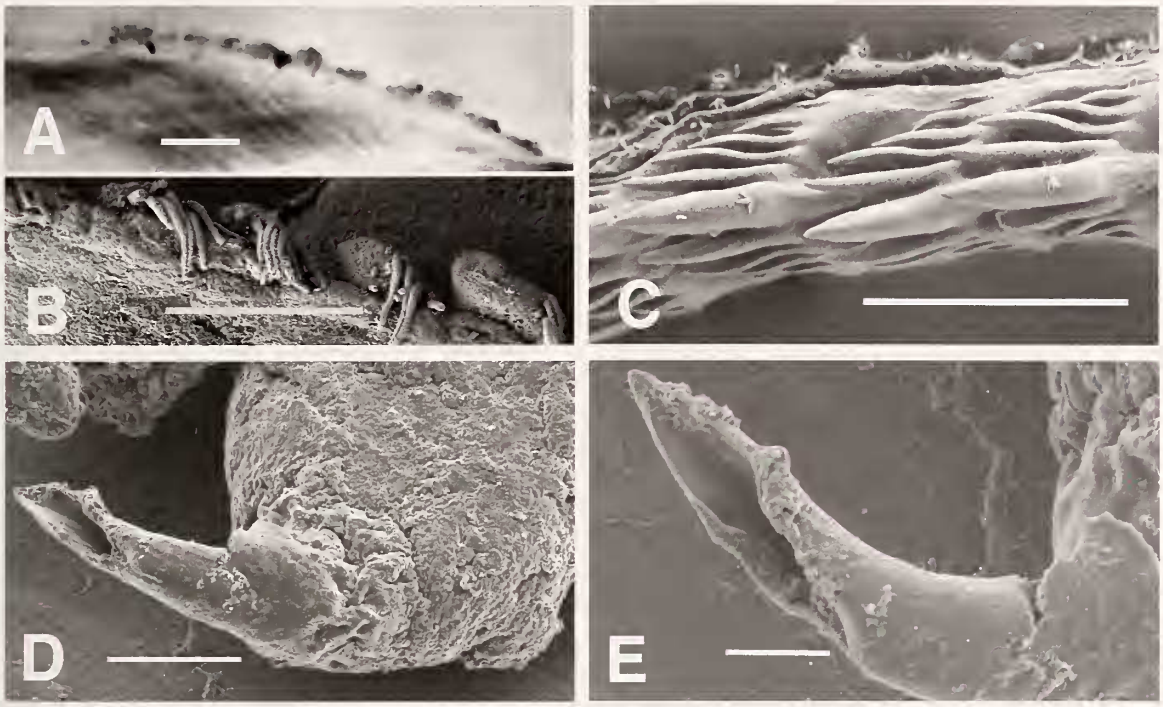

Figure 8. Scanning electron micrographs of *Unidentia angelvaldesi* sp. nov. from Bahía de Banderas, Mexico: **A**, Masticatory flange of a jaw; **B**, Denticles on masticatory margin of jaw; **C**, Radular teeth; **D**, Penis with penial spine; **E**, Close-up of the penial spine. Scale bars: A = 10 μm; B = 10 μm; C = 50 μm; D = 25 μm; E = 10 μm.

Paratypes: LACM 2890, 1 specimen, 6.5 mm long, Los Arcos, El Bajo del Cristo, Bahía de Banderas, 12 June 2003, at 15 m depth, collected by A. Hermosillo. CASIZ 085884, 4 specimens, Dakak, Northern Mindanao, Philippines, 100 m north of lighthouse, 1 April 1993, collected by T. Gosliner. CASIZ 89004, 1 specimen, 9.5 mm, dissected, Tengan Pier, Okinawa, Japan, 19 February 1993, photo 3150D, collected by B. Bolland. LACM 153355, 2 specimens, 3 and 10 mm long, Boca Grande estuary, Bahía Damas, east Isla de Coiba, Panamá, 18 May 2003. **Other material:** 6 specimens, 3 dissected, Los Arcos, La Quijada, Bahía de Banderas, 9 March 2003, 21 m depth, collected by A. Hermosillo. 3 specimens, 2 dissected, Los Arcos, El Bajo del Cristo, Bahía de Banderas, 12 June 2003, at 12 m depth, collected by A. Hermosillo and S. Millen. Futou, Suruga Bay, Japan, 13 October 2002, 3 m depth, photo by J. Imamoto. Bali and Komodo, Indonesia, October 2007, photo by A. Hermosillo.

Etymology: *Unidentia angelvaldesi* is named in honor of Dr. Angel Valdés and his invaluable contributions to the knowledge of the biology, ecology, and taxonomy of the opisthobranchs of the world.

External morphology: The body is long and slender with a preserved maximum size of 9.5 mm, a typical large specimen being 8 × 2 × 2 mm (l × w × h). The living length can be up to 20 mm (Figure 1D, E). The rhinophores are as long as the oral tentacles, up to 3.2 mm in preserved animals, and smooth.

The cerata are arranged in raised, single rows, which slope posteriorly (Figure 7A). The precardiac ceratal rows are on a slight lateral expansion of the body wall. There are 4–6 precardiac rows and 5–8 postcardiac rows. Each row bears up to 12 cerata, a typical formula being 4,4,5,4;7,8,7,6,6,4,3. The cerata are slender and cylindrical, up to 7 mm in length, with moderately long cnidosacs and a wide, irregular core (Figure 7B). The head is oval, wider than long, and equal to the foot width. The mouth is a small, vertical slit. The oral tentacles taper more than the rhinophores and are up to 3.2 mm long in preserved animals. They are slightly flattened on the ventral surface and originate dorsal to the oral surface. The foot is bilabiate but not notched and extended into 1.5-mm-long propodial tentacles. The attached portion of the foot is equal in width to the two moderate lateral flanges and together they are narrower than the body. The trailing portion of the foot is flat, 2.5 mm long, and pointed.

The genital openings have a large, protruding dorsal flap above the female opening. They are located below the third or fourth ceratal row. The anus is on a tall, slender papilla located posterior in the interhepatic space. The opening is anterior to the second to fifth ceras of the first posthepatic row, but the papilla begins

at the base of the row. The renal opening is directly anterior to the anal opening.

Coloration: Two distinct color forms have been observed, one presenting various shades of red and orange (Figure 1D); and a pale, almost white coloration (Figure 1E). In the darkly pigmented animals, the ground color is translucent with a faint red tint with orange or red ovotestis showing through. There are three purple lines running the entire length of the body. One is middorsal, the other two run just underneath the cerata, all three meeting behind the cerata to form a broad strip down the trailing portion of the foot. Opaque white can be found on the dorsal surface, particularly between the tops of the ceratal rows and on the sides of the cephalic area. The bases of the oral tentacles are the ground color followed by bands of opaque white, purple, and opaque white distally. The basal one-third of the rhinophores are the ground color, followed by a band of opaque white, a short band of ground color followed by a short band of purple, and ending in a distal band of ground color with some opaque white specks. The amount of opaque white varies. In some animals it is absent from the oral tentacles and replaced by purple. It often forms mottled rather than solid bands. In one specimen it was light yellow and on the rhinophores it became orange near the purple band. The propodial tentacles have opaque white specks and a purple stripe. The cerata are the same ground color, with cores of darker red, sometimes orange. Below the pale white cnidosacs is a thin band of purple. There is an occasional opaque white spot on the cerata. In the pale specimens, the color of the body and cerata vary from white to white with a purplish tint. It follows the same purple line regime on the body as does the darker variation. The oral tentacles are clear with the distal one-third colored purple. The rhinophores are clear proximally, with a ring of opaque white blotches followed by a purple ring and ending with a clear tip. The cerata are clear, with opaque white cores, a thin purple ring, and clear cnidosacs. A few specimens have pale pink ceratal cores.

Internal anatomy: There are two compact, ramified oral glands lying laterally behind the rhinophores and on either side of the stomach. Ducts enter on each side of the mouth opening. Posterior to the mouth, the anterior portion of the foot has large pedal glands. The buccal mass is oval, with a thin, muscular lip disk over a thin cuticle. The jaws are pale yellow and almost round in shape (Figure 7C). They have a small masticatory margin with one row of up to 22 blunt, jagged denticles (Figure 8A, B). The radular sac has a small projection. The radula has 28–35 median teeth with no lateral teeth. The teeth have a projecting cusp and 4–7 long denticles per side (Figures 7D, 8C). The teeth are approximately 75 µm in length. The posterior limbs articulate with the limbs of the following teeth. The salivary glands are short, wide and leaf-shaped. They have short, narrow ducts leading to the buccal mass. The esophagus is a short tube connected to a large, almost circular stomach. The hepatic ducts are wide leaving either side of the stomach. The posterior duct is dorsal to the ovotestis. The intestine is short, running posteriorly, curving abruptly up to a narrow anal papilla in the posterior interhepatic space. The renal syrinx is just anterior to the intestine, the renal opening is anterior to the anus.

The central nervous system consists of rounded, fused cerebropleural ganglia connected closely together by a wide commissure. The large, short-stalked rhinophoral ganglia lie at the bases of the rhinophores. The well-developed eyes are almost sessile. Small statocysts lie posterior to the eyes. The smaller, somewhat triangular pedal ganglia are ventral, joined to the cerebropleural ganglia by short commissures and to each other by a slightly longer circum-esophageal commissure. The oval buccal ganglia lie next to each other beneath the esophagus.

The reproductive system is illustrated in Figure 7E, F. The ovotestis form what appears to be one irregular mass from the stomach to the end of the body cavity. The female acini are distal to the male acini, which connect to small ducts, which join together. There is a short, narrow hermaphroditic duct that widens into an ampulla with a single tight bend. The long postampullar duct divides into the oviduct and vas deferens. The oviduct is wide, loops, and sometimes becomes swollen. It leads to a large, oval seminal receptacle. It then travels distally as a wide duct to join the female gland mass and continues as a common female duct. The female opening is under a dorsal, projecting flap just posterior to the male opening. There is no distal bursa. The female gland mass has folded mucous glands and an oval, central albumen gland. The vas deferens swells into a prostate after a short distance and forms a short, curved, tubular prostate, then narrows into a short ejaculatory duct, which enters an elongate penial sheath. The penis bears two unequal lobes, the posterior larger than the anterior. Between the lobes is a muscular penial papilla containing the vas deferens. At the opening of the vas deferens is a long, narrow, anteriorly directed, curved stylet (60 µm long) with a slanted opening (Figure 8D, E).

Natural history: This species is known from the tropical Indo- and eastern Pacific. In the Indopacific, from Futou, Suruga Bay, Japan (J. Imamoto, personal communication); Okinawa, Japan; Bali and Komodo, Indonesia; and the Philippines. In the eastern Pacific it has been found from Isla Isabel, Nayarit, Mexico, to Panama. The life cycle of this species has been observed for several yearly cycles in Bahía de Banderas (eastern

Pacific), where it lives on the widespread, orange gymnoblastic hydroid *Corydendrium parasiticum* (Linnaeus, 1767), on which it is very cryptic. The egg mass is 5–6 orange, slightly flattened coils laid in a slightly wavy string on the hydroid with a small capsule-free sheet. It is abundant during the summer months (May, June, and July) and found sporadically throughout the rest of the year. The white specimens from the Indopacific were found feeding on a white gymnoblastic hydroid also belonging to the genus *Corydendrium* Van Beneden, 1844. The difference in body coloration of these specimens indicates this different food source. Not much is known of the life cycle of Indopacific specimens that have been found in May and October.

Discussion: This species has probably long been confused with the similar-looking species *Flabellina rubrolineata* (O'Donoghue, 1929). The most obvious way to distinguish them externally is by the papillate rhinophores and pleuroproctic anus of *F. rubrolineata* opposed to the smooth rhinophores and acleioproctic anus of *Unidentia angelvaldesi*. Internally, the new species has one row of radular teeth as opposed to three found in the genus *Flabellina* Voight, 1834, and the penis is armed with a penial stylet.

The familial and generic placement of this species is problematic. It has the apomorphies of a uniseriate radula and the anus is acleioproctic in position. However, some of the advanced Flabellinidae Bergh, 1899 also have a high anal position close to the acleioproctic one. The reproductive system lacks the apomorphies of the acleioproctic family Tergipedidae, genus *Cuthona* Alder and Hancock, 1855, which has no proximal bursa, and possesses a distal bursa and a penial gland. *Cuthona* also has a shorter and less slender body shape and lacks tentacular propodial tentacles. However, a penial stylet is found in *Cuthona* and several other tergipedid genera.

Edmunds (1970) created the family Piseinotecidae, to separate the genus *Piseinotecus* Marcus, 1955, from the family Tergipedidae. Apomorphies of this genus are one row or tuft arising from the anterior hepatic duct, cerata on lateral projections, the uniseriate radula usually bearing fine denticles and long wings, and with one, proximal bursa. They retain the plesiomorphic feature of hermaphroditic follicles in the gonad. This new animal lacks the ceratal features but has one proximal bursa, a situation found in some Flabellinidae as well as most Facelinidae, all of which have a uniseriate radula but a cleioproctic anal position. Gosliner et al. (2007) produced a cladogram that suggests the genus Piseinotecidae is closest to the family Flabellinidae.

The newly described species possesses a hollow penial stylet at the end of the vas deferens, a situation found in the facelinid genera *Eumarcusia* Roller, 1972, *Nouneaella* Risbec, 1937, most *Herviella* Baba, 1949, *Anetarca* Gosliner, 1991, and *Favorinus* Gray, 1850 (one species). The anal placement in the family Facelinidae is in the apomorphic cleioproct position, between the postcardiac rows. In this new species, the anus is placed in the interhepatic space. The pleisomorphic condition of aeolids is pleuroproct (ventral to the cerata, interhepatic or slightly posterior). However, even in aeolids possessing a triseriate radula, there are several that have acleioproct anal positions (*Cumanotus* Odhner, 1907, some *Flabellina*), so this position appears to be easily derived from the pleuroproct one.

PHYLOGENETIC ANALYSIS

To elucidate the position of the two new genera described in this paper, and to compare the other two species with the types of their genera, a cladogram was generated, based on several previously published aeolid cladograms (Gosliner & Kuzirian, 1990; Wägele & Willan, 2000; Gosliner et al., 2007). The coding information for the 27 species used primarily came from descriptions of Schmekel & Portmann (1982), who provided descriptions of *Calmella cavolini* (Verany, 1846), *Spurilla neapolitana* (Delle Chiaje, 1841), *Berghia verrucicornis* (D. Costa, 1864), *Aeolidiella alderi* (as *sommeringi*) (Cocks, 1852), *Dichata odhneri* Schmekel, 1961, *Facelina auriculata* (O.F. Müller, 1776), *Cratena peregrina* (Gmelin, 1791), *Caloria elegans* (Alder & Hancock, 1845), *Favorinus branchialis* (J. Rathke, 1806), *Doudice* (as *Godiva*) *banyulensis* (Portmann & Sandmeier, 1960), and *Piseinotecus spaerifera* (Schmekel, 1965). Gosliner & Griffiths (1981) was used for *Flabellina capensis* (Thiele, 1925) and Gosliner & Behrens (1986) was used for *Hermosita sangria* Gosliner & Behrens, 1986. *Babakina festiva* (Roller, 1972) came from Roller (1972) and Gosliner et al. (2007), who also described *Babakina indopacifica* Gosliner, Gonzáles-Duarte & Cervera, 2007. *Pruvotfolia pselliotes* (Labbé, 1923) came from Tardy (1970) and *Notaeolidia gigas* Eliot, 1905, from Wägele (1990). Cervera et al. (1987) described *Piseinotecus gaditanus*. Coding information for specimens of *Cuthona punicea* Millen, 1986, *Flabellina verrucosa* (Johnson, 1832), *Doudice occidentalis* (Engel, 1925), *Eubranchus rupium* (Moller, 1842), and *Cumanotus beaumonti* (Eliot, 1906), as well as the four species in this paper, came from personal observation. A total of 27 species were used and 23 morphological characters, which are listed in Table 1 and discussed below. The complete character matrix for the species used is shown in Table 2.

All characters were treated as unordered except for no. 12, the number of lateral radular teeth, which was ordered following Gosliner et al. (2007). Characters were polarized using the primitive aeolid *Notaeolidia*

Table 1

Synopsis of the character states used in the present study.

1. **Notal brim:** 0 = present; 1 = interrupted; 2 = absent
2. **Propodial tentacles:** 0 = absent; 1 = angular; 2 = tentacular; 3 = hooked
3. **Body shape:** 0 = wide; 1 = narrow
4. **Cerata insert:** 0 = arise directly from the notum; 1 = arise from peduncles
5. **Ceratal number:** 0 = fewer than 100 cerata per side;1 = more than 100 per side
6. **First ceratal cluster** (precardiac): 0 = rows; 1 = single arch; 2 = compound arch
7. **Second ceratal cluster** (first postcardiac): 0 – rows; 1 = single arch; 2 = compound arch
8. **Ceratal shape:** 0 = cylindrical; 1 = inflated; 2 = flattened
9. **Anus:** 0 = pleuroproctic; 1 = cleioproctic; 2 = acleioproctic
10. **Rhinophoral base:** 0 = divided; 1 = united
11. **Rhinophoral ornamentation:** 0 = smooth or wrinkled; 1 = annulate; 2 = perfoliate; 3 = papillate; 4 = swollen
12. **Radula:** 0 = multiseriate; 1 = triseriate; 2 = uniseriate
13. **Rachidian tooth shape:** 0 = cuspidate; 1 = pectinate
14. **Rachidian tooth:** 0 = denticulate; 1 = smooth
15. **Rachidian radular teeth:** 0 = symmetrical; 1 = asymmetrical
16. **Jaw denticles:** 0 = multiple rows of denticles; 1 = a single row; 2 = smooth
17. **Reproductive bursae:** 0 = with a distal and a proximal bursa; 1 = with only a distal bursa (Dialauly 1); 2 = with only a proximal bursa (Dialauly II)
18. **Prostate:** 0 = with an enlarged prostate; 1 = without an enlarged prostate
19. **Ejaculatory duct:** 0 = with a muscular ejaculatory portion; 1 = with no distal, muscular narrowing
20. **Penis:** 0 = unarmed; 1 = with cuticular papillae or chitinous hooks; 2 = with a chitinous stylet
21. **Penis shape:** 0 = narrow; 1 = conical; 2 = bulbous
22. **Penial glands:** 0 = absent; 1 = present
23. **Food:** 0 = hydroids; 1 = sea anemones; 2 = opisthobranch eggs

gigas Eliot, 1905, from family Notaeolidiidae Eliot, 1910, as the outgroup species (Wägele and Willan, 2000). Phylogenetic analyses were performed using the program Phylogenetic Analysis Using Parsimony (PAUP), version 4.0b 10 (Swofford, 2002) using the heuristic algorithm (TBR branch swapping option), set at maximum parsimony. Morphological data were compiled using MacClade, version 4.05 (Maddison and Maddison, 2002). Synapomorphies were mapped using the character trace option for unambiguous changes, in MacClade using the single tree from the PAUP analysis (Figure 9). Bremer analyses were performed on this tree to estimate branch support and the numbers are placed on the tree (Bremer, 1994).

CHARACTERS

1. **Notal brim:** 0 = present; 1 = interrupted; 2 = absent. The presence of a notal brim, as is found in *Notaeolidia*, Eliot, 1910 has been considered primitive among the Aeolidacea (Odhner, 1939). A number of species have a discontinuous notal brim, which is thought to be a reduction of the brim; other species have no trace of the notal brim.
2. **Propodial tentacles:** 0 = absent, foot corners rounded; 1 = angular, with tentacles connected by a triangle of tissue; 2 = tentacular, with long extensions; 3 = hooked, with small tentacles. *Notaeolidia* has rounded foot corners. Hooked tentacles are shorter than long propodial tentacles, and angular tentacles have a veil-like connection from the foot to the tentacle. The direction used is that of Gosliner & Kuzirian (1990) and Wägele & Willan (2000).
3. **Body shape:** 0 = wide; 1 = narrow. The direction used is that of Gosliner & Kuzirian (1990) and Wägele & Willan (2000). Wide bodies are found in *Notaeolidia*, *Cumanotus*, and the Aeolidiinae.
4. **Cerata insert:** 0 = arise directly from the notum; 1 = arise from peduncles. Peduncles are found in *Cuthuella* Eliot, 1910 and *Piseinotecus*.
5. **Ceratal number:** 0 = usually fewer than 100 cerata per side of the body; 1 = numerous with many more than 100 per side. Large number of cerata are found on *Notaeolidia gigas* and the Aeolidiidae Odhner, 1907.
6. **First ceratal cluster** (precardiac): 0 = rows; 1 = single arch; 2 = compound arch consisting of more than one cerata per branch laterally or several rows preceding an arch, as in *Facelina auriculata*. Rows, as found in *Notaeolidia*, are considered plesiomorphic. Arches are common in the Facelinidae and Aeolidiidae.
7. **Second ceratal cluster** (first postcardiac): 0 = rows; 1 = single arch; 2 = compound arch consisting of more than one ceras per branch laterally, or several rows preceding an arch as in *Facelina auriculata*. The second cluster usually has fewer

Table 2

Morphological character states used in the phylogenetic analysis.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Notaeolidia gigas	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	2	0	0
Flabellina capensis	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0
Flabellina verrucosa	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0
Calmella cavolini	1	3	1	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0
Babakina festiva	0	2	1	0	0	0	0	0	0	1	2	2	0	0	1	0	0	1	1	0	0	0	0
Babakina indopacifica	0	2	1	0	0	0	0	0	0	1	2	2	0	0	1	0	0	1	1	0	0	0	0
Piseinotecus gaditanus	1	3	1	1	0	0	0	0	2	0	0	2	0	0	0	0	2	0	1	0	0	0	0
Piseinotecus spaerifera	1	3	1	1	0	0	0	0	2	0	0	2	0	0	0	1	2	0	1	0	1	0	0
Cuthona punicea	2	0	1	0	0	0	0	1	2	0	0	2	0	0	0	1	1	1	0	0	1	1	0
Eubranchus rupium	2	0	1	0	0	0	0	1	2	0	0	1	0	0	0	1	1	1	0	2	1	1	0
Cumanotus beaumonti	2	2	0	0	0	0	0	0	2	0	0	1	0	0	0	1	2	0	0	1	2	0	0
Unidentia angelvaldesi	1	2	1	0	0	0	0	0	2	0	0	2	0	0	0	1	2	0	0	2	2	0	0
Spurilla neopolitana	2	1	0	0	1	1	1	2	1	0	2	2	1	0	0	2	2	0	0	0	2	0	1
Berghia verrucicornis	2	1	0	0	1	2	1	0	1	0	3	2	1	0	0	2	2	0	0	0	1	0	1
Aeolidiella alderi	2	1	0	0	1	0	0	2	1	0	0	2	1	0	0	2	2	0	0	0	1	0	1
Dicata odhneri	2	2	1	0	0	1	1	0	1	0	0	2	0	0	0	2	0	0	0	0	0	0	0
Facelina auriculata	2	2	1	0	0	2	2	0	1	0	1	2	0	0	0	1	2	0	1	1	2	1	0
Cratena peregrina	2	2	1	0	0	1	0	0	1	0	0	2	0	0	0	1	2	0	1	0	2	0	0
Pruvotfolia pselliotes	2	2	1	0	0	0	0	0	1	0	1	2	0	0	0	1	2	0	1	1	2	0	0
Caloria elegans	2	2	1	0	0	0	0	0	1	0	0	2	0	0	0	1	2	0	1	1	2	0	0
Favorinus branchialis	2	2	1	0	0	1	1	0	1	0	4	2	0	1	0	0	2	1	0	0	0	0	2
Adfacelina medinai	2	2	1	0	0	2	2	0	1	0	2	2	0	0	0	1	2	0	1	1	2	0	0
Dondice banyulensis	2	2	1	0	0	2	2	0	1	0	1	2	0	0	0	1	2	1	1	0	1	0	0
Dondice galaxiana	2	2	1	0	0	2	2	0	1	0	1	2	0	0	0	1	2	0	1	0	2	1	0
Dondice occidentalis	2	2	1	0	0	2	2	0	1	0	1	2	0	0	0	1	2	1	1	0	2	1	0
Hermosita sangria	2	2	1	0	0	1	1	0	1	0	2	2	0	0	0	2	0	0	1	0	1	0	0
Hermosita hakunamatata	2	2	1	0	0	1	1	0	1	0	2	2	0	0	0	1	0	0	1	0	1	0	0

cerata than the first, and *Berghia verrucosa* on pg 159 changes from a double to a single arch, while *Cratena peregrina* changes from a single arch to rows.

8. **Ceratal shape:** 0 = cylindrical; 1 = inflated; 2 = flattened. Most aeolids have cylindrical cerata, but they are inflated in *Cuthona* and *Eubranchus* Forbes, 1838 and basally flattened in *Aeolidiella* Bergh, 1867 and *Spurilla* Bergh, 1864.
9. **Anus:** 0 = pleuroproctic; 1 = cleioproctic; 2 = acleioproctic. *Notaeolidia* is pleuroproctic, as are *Flabellina* species, *Calmella*, and *Babakina* Roller, 1973. *Cuthona*, *Eubranchus*, *Cumanotus*, *Piseinotecus*, and *Unidentia* are acleioproctic, whereas the rest of the aeolids are cleioproctic.
10. **Rhinophoral base:** 0 = divided; 1 = united. The united base is an apomorphy of the genus *Babakina*.
11. **Rhinophoral ornamentation:** 0 = smooth or wrinkled; 1 = annulate, with a series of rings; 2 = perfoliate with sloping lamellae; 3 = papillate, with papillae; 4 = swollen, with one or more swellings along the length. *Notaeolidia gigas* has annulate rhinophores, but the absence of increased surface area on smooth rhinophores is considered plesiomorphic.
12. **Radula:** 0 = multiseriate with several rows of lateral teeth; 1 = triseriate with a lateral tooth on each side of the rachidian tooth; 2 = uniseriate, with only a rachidian row. See Wägele & Willan (2000) and Gosliner et al. (2007). This character has been treated as ordered as in Gosliner et al. (2007).
13. **Rachidian tooth shape:** 0 = cuspidate, with a series of denticles flanking a triangular cusp; 1 = pectinate, with larger comb-like denticles flanking a small central cusp. The latter is found in the Aeolidiidae.
14. **Rachidian tooth:** 0 = denticulate; 1 = smooth. This is an apomorphy for *Favorinus*.
15. **Rachidian radular teeth:** 0 = symmetrical, with the same number of denticles on either side of the cusp; 1 = asymmetrical, with different numbers of denticles on either side of the cusp. The latter is an apomorphy for some species of *Babakina* (Gosliner et al. 2007).
16. **Jaw denticles:** 0 = with multiple rows of denticles on the masticatory margin; 1 = with a single row of denticles; 2 = smooth, without denticles. Although *Notaeolidia gigas* has a smooth masticatory margin, multiple rows of denticles as found

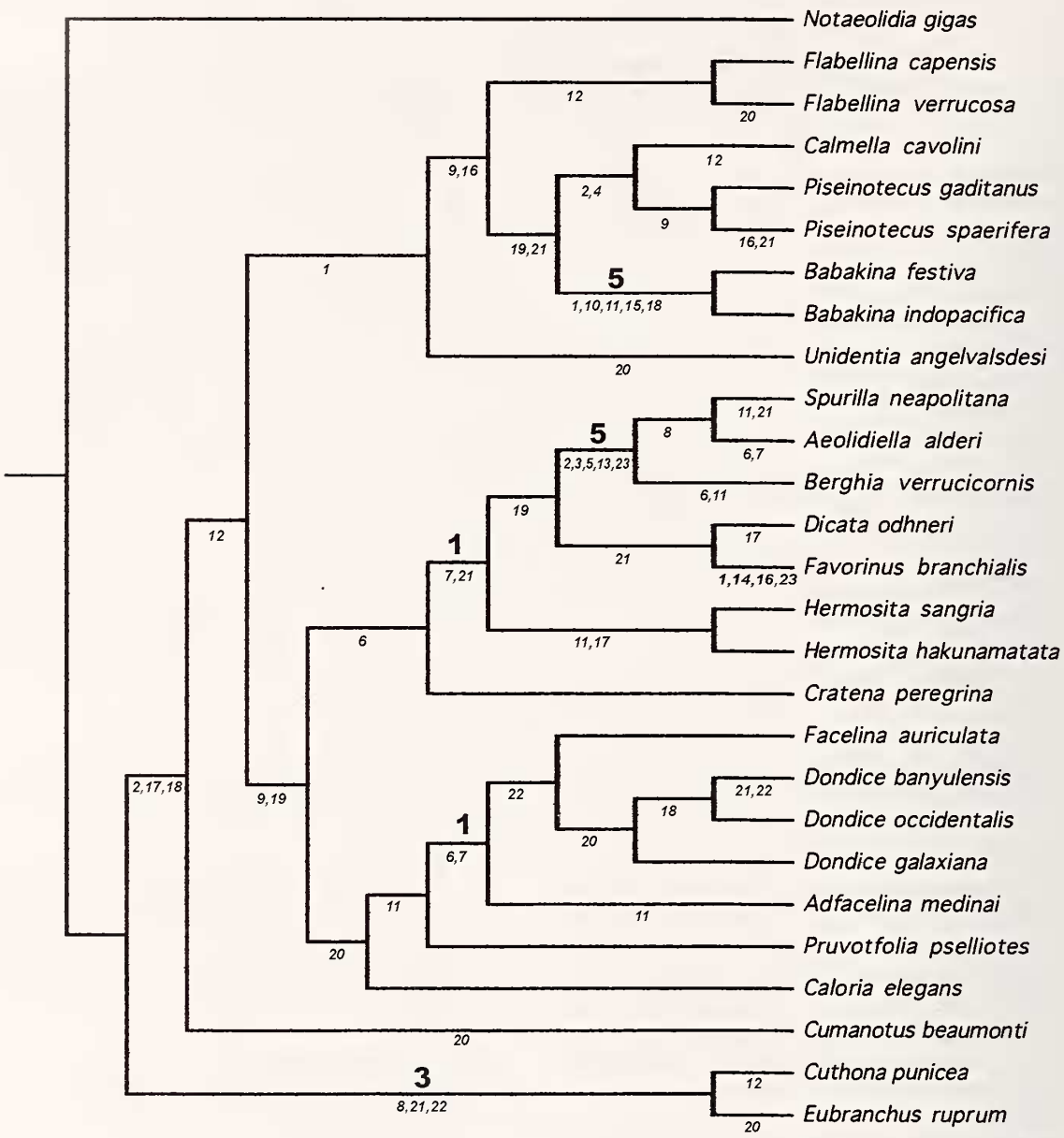

Figure 9. Single tree obtained from the analysis of the characters listed in Table 1 and the matrix in Table 2. Character numbers are plotted below the line in lowercase italics; larger numbers above the line represent Bremer support values.

in *Flabellina*, *Calmella*, and *Babakina* are considered plesiomorphic.

17. **Reproductive bursae:** 0 = with a distal and a proximal bursa; 1 = with only a distal bursa (Dialauly 1); 2 = with only a proximal bursa (Dialauly II). As pointed out by Wägele & Willan (2000), the functions of the distal bursa may differ. The proximal bursa, when present, is always a receptaculum seminis. The presence of both a proximal and a distal bursa is considered plesiomorphic by Wägele & Willan (2000).
18. **Prostate:** 0 = with a widening of the vas deferens into an enlarged prostate; 1 = without a widening of the vas deferens into an enlarged prostate. The presence of a widened prostatic portion of the vas deferens is considered plesiomorphic by Gosliner et al. (2007).
19. **Ejaculatory duct:** 0 = with a distal narrowing between the prostate and penis to form a muscular ejaculatory portion of the vas deferens: 1 = with no distal, muscular narrowing between the prostate and the penis.

20. **Penis:** 0 = unarmed and smooth; 1 = armed with cuticular papillae or chitinous hooks; 2 = armed with a chitinous stylet. Most species have an unarmed penis, but it is not clear at present whether hooks and papillae which may or may not be chitinous are homologous. A stylet of chitin is found in some *Eubranchus* species and *Unidentia*.
21. **Penis shape:** 0 = narrow, not tapering; 1 = conical, wider proximally, with a narrow tip; 2 = bulbous, wide, with a wide tip. The directionality is as in Gosliner et al. (2007).
22. **Penial glands:** 0 = absent; 1 = present as a secondary structure to the penis. Glands found in *Eubranchus*, *Cuthona*, and *Dondice* may replace prostatic portions of the vas deferens. The function of the gland entering the penial sheath in *Facelina* may not be homologous.
23. **Food:** 0 = hydroids; 1 = sea anemones; 2 = opisthobranch eggs. Most aeolids feed on hydroids, but the Aeolidiidae feed on sea anemones. *Favorinus* feeds on opisthobranch eggs.

The single tree derived from the analysis is shown in Figure 9. It has a length of 78 steps and a consistency index of 0.50, a retention index of 0.7068, and a homoplasy index of 0.50. Bremer values are generally weak, most nodes are unsupported, but a few are strong (5). These values are plotted onto Figure 9.

PHYLOGENETIC DISCUSSION

Two other cladograms have been published that encompass a large number of aeolid genera, with *Notaeolidia* as the basal genus. Wägele & Willan (2000) have a large tree with a subset of seven aeolid genera, four of which are included here. The basic tree pattern is similar in that both phylogenies indicate that a clade, containing sister families (Bremer support value 3), Eubranchidae Odhner, 1934, and Tergipedidae Bergh, 1889, diverged from the rest of the aeolids. In their tree, the first branch is the clade of family Flabellinidae Bergh, 1899. A sister clade to the *Cuthona*, *Tergipes* Cuivier, 1805, *Eubranchus* clade is a clade that contains members of two large families, the Facelinidae Bergh, 1890, and the family Aeolidiidae Grey, 1827. Gosliner et al. (2007) present a consensus tree based entirely on aeolids, with 15 of the genera in common with our analysis to which we have added six others. Their analysis did not contain the genera *Cuthona* and *Eubranchus* or the family Cumanotidae Odhner, 1907. In our analysis, all three genera branched off early from the rest of the aeolids. Their first branch is that of the Flabellinidae, which agrees with this analysis in that it is in the same clade and basal to the genera *Calmella* and *Piseinotecus*. They found *Babakina* formed a separate clade. In our analysis, *Babakina* is well separated (Bremer support 5) but appears to be intermediate between *Flabellina* and the *Calmella–Piseinotecus* genera. This clade is joined basally by a new sister genus *Unidentia* in the newly created family Unidentidae.

The majority of aeolids in this analysis belong to the family Facelinidae. This analysis, consistent with that of Gosliner et al. (2007), does not support the Facelinidae as a clade. Instead, the Facelinidae are found in two weakly separated sister clades and the family Aeolidiidae is nested within one of these clades, with strong Bremer support values (5) for the Aeolidiidae. This combined clade, containing family Aeolidiidae, is supported by character 6, precardiac cerata in single arches, and with the exception of *Cratena peregrina*, character 7, postcardiac cerata in simple arches. It also contains the newly reassigned species *Hermosita hakmamatata*, which is a sister species to *Hermosita sangria*. The second facelinid clade is separated by character 20, an armed penis. Most species in this clade have a compound pre- and postcardiac arch, characters 6 and 7 (Bremer support value 1). Within this clade, the new species *Dondice galaxiana* is basal to *Dondice banyulensis* and *Dondice occidentalis*, and is thus correctly placed in this genus. The new genus and species *Adfacalina medinai* is basal to *Facelina* and the genus *Dondice*, and appears to be allied to these two genera.

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